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Invited Review

Dear enemies or nasty neighbors? Causes and consequences of variation in the responses of group-living species to territorial intrusions

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Territorial behavior is widespread throughout the animal kingdom, with responses to conspecific intruders differing depending on various ecological, life history, and social factors. One factor which has received considerable research attention is rival identity. Early work provided many examples of species exhibiting relatively stronger responses to strangers versus neighbors (the “dear-enemy” effect) or the opposite (the “nasty-neighbor” effect). However, those studies focused predominantly on single or pair-bonded territory-holders. There is increasing evidence of neighbor–stranger response differences in group-living species (where 3 or more individuals share a territory), and of within-species variation in the relative responses shown to these 2 intruder types. Considering social species is important both because group territoriality is widespread and because group responses include the actions of multiple individuals whose interests and motivations differ. We begin our review with a summary of territoriality in group-living species. We then discuss causes of variation in territorial responses depending on intruder neighbor–stranger identity, considering both between-species differences and those within species arising from context-dependent variation and from individual group members responding differently to the same intrusion. We next detail the consequences of different territorial responses, in terms of both postinteraction behavior and individual benefits and costs. Finally, we suggest 3 key areas—theoretical modeling, hormonal mechanisms, and anthropogenic disturbances—that could be developed when considering the relative responses of territory-holders to neighbors and strangers. Since conflict is a powerful selective force, determining the causes and consequences of variation in group-territorial behavior is important for a full understanding of sociality.

Key words: conflict, defense, discrimination, identity, neighbors, recognition, signals, sociality, strangers, territoriality.

INTRODUCTION

Territoriality is a widespread phenomenon in the animal kingdom, occurring in a diverse array of taxa including mammals, birds, fishes, reptiles, amphibians, crustaceans, and insects (Brown and Orians 1970; Stamps 1994). **Territories** are spatial areas defended against conspecifics (see Table 1 for definitions of key terms, which are highlighted in bold on first mention), for exclusive access to resources such as food and water, breeding and sleeping sites, and mates. **Defensive responses** can involve a range of tactics including visual, vocal or olfactory cues and signals, ritualistic displays, and physical aggression. Such responses to territorial **intruders** can differ depending on a variety of ecological, life history, and social factors, with **rival** identity one factor that has received considerable research attention. In particular, an extensive literature exists on the different responses shown to **neighbors**

compared to non-neighbors or “**strangers**” (Ydenberg et al. 1988; Temeles 1994; Hyman 2005; Radford 2005; Müller and Manser 2007; Monclús et al. 2014; Moser-Purdy et al. 2017a).

The most commonly evoked adaptive explanation for neighbor–stranger response differences (NSRD) by territory-holders is that these 2 intruder types pose a different level of threat (Temeles 1994). Neighbors could be less threatening for 2 main reasons. First, because they are known to be present at a regular border, whereas intrusions by strangers are spatially and temporally more unpredictable (Jordan et al. 2007). Second, because potential resource losses to neighbors may be less than those to strangers; for instance, in the breeding season, neighbors already own a territory and thus are only seeking mating opportunities, whereas strangers could additionally be looking to usurp the territory-holder permanently (Wilson 1975). In such cases, a lesser response to neighbors cf. strangers is expected; a difference known as the “**dear-enemy**” (**DE**) effect (Fisher 1954). By contrast, there are situations where neighbors may represent a greater threat than strangers, because

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Table 1.
Definitions of key terms used throughout the review

Term	Definition
Dear-enemy (DE) effect	Relatively stronger defensive responses to territorial intrusions by strangers vs. neighbors.
Defensive response	Immediate behavioral reactions to intruders or to evidence of their recent presence (e.g., scent marks).
Group	Three or more individuals who share a territory.
Intruders	Conspecific outsiders who encroach on the territory held by another individual, mated pair or group.
Nasty-neighbor (NN) effect	Relatively stronger defensive responses to territorial intrusions by neighbors vs strangers.
Neighbors	Conspecifics who own territories adjacent to one another (i.e. have a shared boundary).
Postinteraction behavior	Behavior in the aftermath of defensive responses to intruders or to evidence of their recent presence.
Rivals	Conspecific individuals, mated pairs or groups competing for the same resources.
Strangers	Conspecifics who do not own territories with shared boundaries (i.e., individuals, mated pairs or groups from further afield).
Territory	Spatial area defended by individuals, pair or groups against conspecifics for exclusive access to resources.

potential losses to them exceed those to strangers. For example, if fluctuating food levels on feeding territories encourage usurpation by neighbors (Temeles 1990) or if transient strangers are smaller and less motivated to encroach than neighbors (Müller and Manser 2007). In these cases, a greater response to neighbors cf. strangers is expected; a difference referred to as the “**nasty neighbor**” (NN) **effect** (Müller and Manser 2007).

Early work provided many examples of both the DE and NN effects in species where single individuals or mated pairs defend a territory; species with these social structures accounted for the vast majority of those considered in a seminal review of the subject (Temeles 1994). But, in recent years, there has been increasing evidence that NSRD also occur in a wide range of species that live in **groups**, which we here define as those where 3 or more individuals (often 10s or even 100s) share a territory (Radford 2005; Müller and Manser 2007; Herbinger et al. 2009; Newey et al. 2010; Bruintjes et al. 2016). Considering such species is important not only because group territoriality is widespread, but because territorial responses of groups are made up of the actions of multiple individuals whose interests and motivations differ; while this is also true to some extent in pair-bonded species, many additional factors can vary in groups of 3 or more. The relative level of threat from neighbors and strangers, and ensuing contributions to contests by territory-holders, may differ depending on individual characteristics such as gender, dominance status and dispersal likelihood, within-group punishment and rewards, and competition for resources among groupmates (Radford 2003; Kitchen and Beehner 2007; Abbink et al. 2010; Barker et al. 2012; von Rueden et al. 2015). Moreover, the consequences of territorial conflict in group-living species include not only those apparent when considering disputes between solitary territory holders (e.g., risk of injury, loss of time, changed space use), but also effects on within-group behavioral interactions, group dynamics, and collective decision-making (Radford and Fawcett 2014; Radford et al. 2016), all of which may influence individual fitness. Since conflict is recognized as a powerful selective force, determining the causes of variation in group-territorial behavior and the resulting consequences is important for a full understanding of sociality.

Here, we begin by providing a brief overview of territoriality, intrusion threats, and NSRD in group-living species. We then discuss causes of variation in territorial responses depending on intruder neighbor–stranger identity, considering both between-species differences and those within species arising from context-dependent variation and from individual group members responding in different ways to the same intrusion. Setting the scene with empirical examples from species where single individuals and mated pairs defend territories, we make predictions for group-living species. We next detail the

consequences of different responses to intruders, in terms of both **postinteraction behavior** (within-group interactions, movement patterns, resource use, and decision-making) and the resulting benefits and costs for individuals. Finally, we suggest 3 key areas—theoretical modeling, hormonal mechanisms, and the potential impact of anthropogenic disturbances—that, along with their experimental testing, could usefully be developed in future work on the relative responses of territory-holders to neighbors and strangers.

TERRITORIALITY IN GROUP-LIVING SPECIES

From hymenopterans to humans, animals live and interact in groups. In many of those species, individuals defend a communal territory containing resources critical for reproduction and survival. Groups face a variety of potential threats from conspecific intruders. Rival groups might attempt to acquire particular resources, such as feeding or breeding sites, or take-over an entire territory (Radford 2003; Wilson and Wrangham 2003; Kitchen and Beehner 2007); in these cases, there may be a cost to all or most group members and so an incentive for shared defense. Alternatively, same-sex coalitions may look to usurp equivalent sub-groups and gain access to members of the opposite sex (Doolan and Macdonald 1996; Ridley 2012), while individual intruders may challenge the breeding success of certain group members (Mares et al. 2011; Bruintjes et al. 2016). In these latter cases, the threat posed is not the same for all members of the territory-holding group and so there are more varied incentives to participate in defensive actions. In general, therefore, the identity of the intruder influences the nature and level of threat and thus the resulting responses. Whether intruders are from neighboring territories or further afield is one such identity factor that has been demonstrated to be of importance (Radford 2005; Müller and Manser 2007; Herbinger et al. 2009; Newey et al. 2010; Bruintjes et al. 2016).

Territory-holders may encounter actual intruders or evidence of their recent presence (e.g., scent-marks). In both cases, successful discrimination of neighbors and strangers requires the existence of reliable indicators of identity. Intruder neighbor–stranger identity could be discerned through a range of sensory modalities, including sound and smell (Radford 2005; Müller and Manser 2007). For instance, group members of many social bird species combine in the production of vocal choruses, which can have distinctive group-specific signatures (Baker 2004; Radford 2005). Playback experiments have demonstrated that territory-holders can distinguish both between neighbors and strangers and between different neighbors based solely on these acoustic cues (Radford 2005). In social

mammals, NSRD have been found in response to just fecal deposits, secondary olfactory cues of rival intrusion (Müller and Manser 2007). Group-specific odors may be underpinned by differences in symbiotic bacteria found in glandular secretions (Theis et al. 2012; Leclaire et al. 2014). Discrimination may also extend to individual intruders from different groups, if they produce a cue to group membership or can be individually recognized and territory-holders have learnt to which group they belong (Cheney and Seyfarth 1982; Herbinger et al. 2009). Even without sensory indicators of identity, some discrimination of neighbors and strangers might arise from differences in familiarity; territory-holders will generally have more knowledge about neighbors than strangers (Getty 1987).

Responses to intruders encompass both information gathering and attempts to win contests, and thus evict rivals. There may be vocal exchanges (Radford 2003; Bradley and Mennill 2009) or inspection of fecal deposits (Müller and Manser 2007; Mares et al. 2011) to garner information about, for instance, the number of intruders, group composition and the level of motivation, as well as potential opportunities for dispersal and extra-group matings (Lazaro-Perea 2001; Radford and du Plessis 2004a; Humphries et al. 2015). Contests, which involve direct and discrete behavioral interactions, may escalate from displays to chasing to physical fights; as with all animal contests, the latter are usually a last resort when an outcome has not been reached by less costly means (Hardy and Briffa 2013). Variation in response to neighbors and strangers can therefore be expressed in many ways, including the speed and intensity of the initial reaction, the duration of involvement, and the level of escalation. Such variation, both to different intruders and to the same intruders on different occasions, may have a range of causes and consequences, which we explore in the next 2 sections.

CAUSES OF DIFFERENCES IN TERRITORIAL RESPONSE

Traditionally, studies have considered between-species differences in the responses elicited by neighbor and stranger intrusions (Temeles 1994). Species were thought to exhibit either the DE or the NN effect when comparisons of different intruders demonstrated a stronger response to one or other type; cases where responses to neighbors and strangers appeared similar (e.g., Battiston et al. 2015; Christensen et al. 2016) could be because there is no actual difference in relative threat posed, be the consequence of low statistical power or, in the case of group-living species, result from different individuals responding differently to the same intrusion. Within-species variation in responses to neighbor-stranger intrusions is, however, also likely; there is increasing evidence from species where single individuals or mated pairs defend territories that responses may differ between populations, between territory-holders within the same population, and even for the same territory-holders under different ecological and social circumstances (Hyman 2005; Briefer et al. 2008; Yoon et al. 2012; Monclús et al. 2014). Such within-species variation is expected in group-living animals, both because of differences in context across time or space, and because individual group members (differing in, for example, sex, dominance status, and age) may respond differently to the same intrusion; we consider both possibilities below.

Between species

As with solitary and pair-bonded species, there are examples of both DE and NN effects in group-living animals. Green

woodhoopoes (*Phoeniculus purpureus*), for instance, exhibit the DE phenomenon (Radford 2005). Groups responded less intensively to the playback of choruses from neighboring groups on the expected territory boundary compared to choruses from strangers (Radford 2005), a difference in response that is in line with the relative threat posed by these 2 intruder types in this species. Neighboring woodhoopoe groups winning a between-group conflict only temporarily forage and examine roost holes before returning to their own territory (Radford and du Plessis 2004a)—there are no permanent changes in the territory boundaries (Radford and du Plessis 2004b)—but groups have been known to lose their territories permanently to strangers (Ligon and Ligon 1990). Experimental work has also demonstrated a heightened response of Eurasian badgers (*Meles meles*) to the scent-marks of strange groups compared to those of neighbors (Palphramand and White 2007).

By contrast, banded mongooses (*Mungos mungo*) provide a classic example of the NN effect (Müller and Manser 2007). Groups responded more strongly to olfactory cues (experimentally presented scent-marks) of their neighbors on the expected territory boundary than to those of strangers. Again, differing threat levels provide a plausible ultimate explanation: banded mongoose neighbors may potentially usurp territory-holders, engage in lethal fights and compete for mates (Cant et al. 2002), whereas strangers commonly represent small, single-sex groups of dispersers that are typically outnumbered (Cant et al. 2001). A NN effect has also been demonstrated in other group-living species where neighbors represent a greater threat than strangers: for instance, chimpanzees (*Pan troglodytes*; Herbinger et al. 2009), the cooperatively breeding cichlid *Neolamprologus pulcher* (Bruitjes et al. 2016) and various social insects, including weaver ants (*Oecophylla smaragdina*; Newey et al. 2010), Japanese queenless ants (*Pristomyrmex pungens*; Sanada-Morimura et al. 2003), and termites (*Nasutitermes corniger*; Dunn and Messier 1999). When more studies on group-living animals have been conducted, quantitative assessments of the relative occurrence of DE and NN effects in species with different social structures will be feasible; an early review of the subject indicated that the DE phenomenon may be the most common scenario in solitary and pair-bonded species (Temeles 1994), while it has been suggested that the NN effect may predominate in social species (see Müller and Manser 2007; Newey et al. 2010).

Within species: context-dependent variation

In species where single individuals or mated pairs defend territories, conditional responses to neighbors and strangers have been found depending on population density. Such differences can be apparent when comparing different populations: for example, in orange-crowned warblers (*Oreothlypis celata*), neighbors elicited a stronger response than strangers in a population with high breeding densities, whereas the DE effect was found in a lower-density population (Yoon et al. 2012). Within-population variation in territory density has also been shown to influence relative responses to neighbors and strangers: for instance, experimental manipulations in sand fiddler crabs (*Uca pugilator*), where individual males defend territories, demonstrated that the DE phenomenon was greatly lessened with increasing proximity of neighboring nests (Pratt and McLain 2006). Similar effects of population density might be expected in group-living species. Between-population variation in the spatial patterning of territories exists in green woodhoopoes, for example: territories in South Africa tend to be arranged linearly along forested river courses, with only one neighbor at either end (Radford and du Plessis 2004b), whereas territories in Kenya can

be surrounded by several others in more open woodland habitat (Ligon and Ligon 1990). It might therefore be predicted that the DE effect seen in South Africa (Radford 2005) may be a NN one in Kenya. Where group-territorial species exhibit within-population variation in density—as is the case in badgers and lions (*Panthera leo*) (Rogers et al. 1997; Packer et al. 2005)—equivalent predictions about the relative level of DE and NN effects might be made.

Seasonal changes in social context can influence the threat posed by different outsiders to individual and mated-pair territory-holders, resulting in conditional responses to neighbors and strangers (Hyman 2005; Briefer et al. 2008; Moser-Purdy et al. 2017a). Such changes might relate to territorial stage and stability. For instance, Carolina wrens (*Thryothorus ludovicianus*) showed the DE effect in spring, when territories have been established for several months; by contrast, following a new influx of birds in the autumn, there was no difference in response to neighbors and strangers that presumably present an equivalent threat at this stage (Hyman 2005). Seasonal changes might also relate to timing in the breeding cycle. Male song sparrows (*Melospiza melodia*), for example, displayed a DE effect only when their female was not fertile; during the fertile period, neighbors and strangers represent a similar threat to paternity (Moser-Purdy et al. 2017a). In group-living species, there are seasonal fluctuations in overall levels of responses to territorial intrusions, potentially because of changes in resource value, time and energy available for defense, and period in the breeding cycle (Jordan et al. 2007; Golabek et al. 2012). For example, pied babbler (*Turdoides bicolor*) groups interacted with rivals less and responded less strongly to an experimentally simulated intrusion of neighbors in nonbreeding periods compared to the breeding season (Golabek et al. 2012). It is therefore plausible that social species could exhibit seasonal fluctuations in relative responses to neighbors and strangers; to our knowledge, this remains to be tested.

The DE phenomenon rests on the assumption of mutually agreed boundaries being respected (Wilson 1975; Godard 1993), and thus repeated intrusions by particular neighbors can cause a breakdown in this relationship with those rivals. Individual and mated-pair territory-holders have been found to become more aggressive toward previously tolerated neighbors in a range of fishes (Akçay et al. 2009; Aires et al. 2015), birds (Godard 1993; Hyman and Hughes 2006) and mammals (Monclús et al. 2014). For example, repeated presentations of neighbor fecal pellets in European rabbit (*Oryctolagus cuniculus*) territories resulted in an increasingly strong response (Monclús et al. 2014). Experiments testing the effect of previous experience have highlighted the possibility of true individual recognition, meaning defenses can be adjusted depending on the specific intruder and the relative threat that they pose (Carazo et al. 2008; Akçay et al. 2009). For instance, differences in response to more and less aggressive neighbors were found in song sparrow males (Hyman and Hughes 2006). In group-living species, there is also variation in the frequency of intrusions and levels of aggressiveness by different neighbors (Radford 2008a; Mitani et al. 2010). Moreover, there is evidence that different groups and their members can be distinguished from vocal and olfactory cues (Cheney and Seyfarth 1982; Radford 2005; Theis et al. 2012; Leclaire et al. 2014). In principle, it is thus possible that defensive responses could be tailored to the threat level presented by different neighbors.

Other characteristics of the rivals may combine with neighbor-stranger identity to influence the response of territory-holders. For example, the resource-holding potential (RHP), functionally defined as the relative fighting ability of a contestant (Parker 1974), can influence threat level. In solitary species, RHP may differ depending

on age (Arcese 1987) and body size (Metcalfe et al. 2003), whereas group size is often important in social species. Larger groups have been shown to dominate smaller ones in the between-group encounters of a range of species (Cant et al. 2002; Radford and du Plessis 2004a). Thus, larger neighboring groups may be more threatening than smaller stranger groups, or vice versa; the threat of particular neighbors might also change over time with changing group size. Since species can potentially use acoustic information to assess group size (McComb et al. 1994) as well as neighbor-stranger identity (Radford 2005), early decisions about response levels relating to various characteristics of rivals may be possible.

Aspects of the interaction between territory-holders and rivals, such as encounter location, may also affect the defensive response exhibited. The core of a territory is generally more valuable to residents than border regions (Falls 1982; Giraldeau and Ydenberg 1987), and increased aggression when encountering intruders in the core has been demonstrated in various solitary species (Goldman 1973; Bolyard and Rowland 2000; Carazo et al. 2008). In group-living species too, encounter location matters (Furrer et al. 2011; Crofoot et al. 2008). In white-faced capuchins (*Cebus capucinus*), for instance, smaller resident groups outcompete larger intruder groups when conflict takes place on home-ground, presumably because they have more to lose and consequently act more aggressively (Crofoot et al. 2008). Neighboring groups encountered on the opposite side of a territory to where they reside are often met with the same level of aggression as strangers (Radford 2005; Müller and Manser 2007; Akçay et al. 2009). Improving our understanding of NSRD therefore requires consideration of combinations of factors as they rarely, if ever, are occurring in isolation.

Within species: within-group variation

In pair-bonded territorial species, there is extensive evidence of sex-based variation in responses depending on intruder sex; breeders of the same sex as the intruder often, but not always, show a stronger defensive reaction than their partner (see Langmore 1998; Hall 2004). Individuals in group-living species differ not just in sex, but also in, for instance, dominance status, age, queue position and likelihood of inheritance, as well as within-group breeding opportunities. It is well established that, in general, individual members of groups can consequently differ in their responses to the same territorial intrusion (Heinsohn and Packer 1995; Radford 2003; Kitchen and Beehner 2007; Desjardins et al. 2008); at least some of these differences are likely related to intruder neighbor-stranger identity.

In terms of information-gathering during interactions with intruders or with cues of their recent presence, within-group differences may be because future opportunities arising from dispersal, extra-group copulations or the arrival of new group members are not the same for all individuals (Lazaro-Perea 2001; Radford and du Plessis 2004a; Humphries et al. 2015). For instance, potential dispersal opportunities to neighboring groups are likely less obvious or nonexistent with strangers (Bowler and Benton 2005), and so more variation between group members in information-gathering might be expected during interactions with neighbors. In terms of threats from individual outsiders, the greatest within-group variation in response is expected when particular group members stand to lose the most. For example, when there is an external challenge to a dominance position or to mating success, the strongest response is expected from same-sex breeders; this general prediction is supported by empirical work on meerkats (*Suricata suricatta*) and cichlid fish (Desjardins et al. 2008; Mares et al. 2011). In the cichlid

Neolamprologus pulcher, new group members tend to have dispersed from neighboring rather than stranger groups (Stiver et al. 2004). Thus, there may be a strong NN effect from those individuals (e.g., same-sex breeders) who are most threatened by an immigration event, but no such NSRD from others in the group. The same intruder could also provide opportunities to some and threats to others. In cooperatively breeding striped mice (*Rhabdomys pumilio*), for example, males display a stronger territorial response towards neighbors, especially in the breeding season, while young females actively seek out copulations with neighbors to increase their fitness (Schradin et al. 2012).

Even when defense is about protecting shared resources, variation in the involvement of group members can occur for many reasons, including differences in endowment (e.g., physical size, strength and condition, personality), individual costs of effort, and expected gains from cooperation or losses from intruder success (Gavrilets 2015; von Rueden et al. 2015). Often, therefore, the greatest contributors to group defense are those with the largest endowment, who can participate at the least cost, and who will gain the most from winning (Watts and Mitani 2001; Mares et al. 2011; Willems et al. 2015). In those species where strangers represent the greater threat (Radford 2005; Palphramand and White 2007), the stronger defense response to them rather than neighbors might result either from all responders contributing more or from a larger proportion of the territory-holding group participating. The DE effect might therefore only be predicted in those individuals who respond solely or mostly to strangers, whereas those group members always engaging in defense may not show such a strong response difference to the 2 types of intruder. Moreover, if neighbors and strangers are intruding for different reasons, then further variation in responses might be expected: for instance, in species where both sexes engage in defensive actions, stronger male involvement might be predicted when the threat is to sexual access to females, whereas greater female involvement might occur when access to food, water or shelter could be lost (Majolo et al. 2005). Since the interests of different group members are not perfectly aligned, collective action problems (CAPs) can arise with respect to territorial defense (Willems et al. 2013). CAPs characterize situations in which group members can make individually costly contributions towards a collective good (e.g., a territory), but because individuals can potentially receive benefits without contributing (i.e., there can be “free-riding”), they have an incentive to reduce their efforts or not help at all (Olson 1965; Gavrilets 2015). How neighbor–stranger identity influences CAPs remains to be explored.

CONSEQUENCES OF DIFFERENCES IN TERRITORIAL RESPONSE

The main focus of studies into NSRD has been on the immediate information-gathering and defensive responses elicited by intruders and cues of their presence. There has been less investigation of how neighbor–stranger identity influences postinteraction behavior, despite such behavioral changes being recognized as generally common in individual, pair-bonded and group territory-holders, and being potentially longer-lasting than defensive acts (Mougeot et al. 2002; Descovich et al. 2012; Radford et al. 2016). In group-living species, postinteraction behavior also relates to key aspects of sociality such as CAPs, punishment and consensus decision-making (Radford and Fawcett 2014; Willems et al. 2015; Radford et al. 2016). Both defensive and postinteraction behaviors have fitness consequences for those involved (Grinnell et al. 1995; Mares et al.

2012; Hardy and Briffa 2013), so considering individual benefits and costs is crucial for a full understanding of variation resulting from intruder neighbor–stranger identity.

Postinteraction behavior

Territorial intrusions have been shown to influence a range of postinteraction behaviors in species where either individuals or mated pairs defend a territory. For instance, studies have demonstrated increased levels of vigilance (Olendorf et al. 2004; Descovich et al. 2012), increased hiding behavior and reduced movement (Descovich et al. 2012), and increased patrolling of the area in which interactions occurred (Arnold et al. 2011). In pair-bonded species, territorial intrusions can affect behavior between the male and female partners (Mougeot et al. 2002; Snijders et al. 2017). There is increasing evidence that territorial intrusions in general also have effects on subsequent behavior in group-living species (Radford et al. 2016). For example, there can be increases in affiliation (Radford 2008a; Brintjes et al. 2016) or aggression (Polizzi di Sorrentino et al. 2012) between group members following encounters with intruders or their cues. Such changes may be the proximate consequence of increased stress levels, and may function to reward or punish group members depending on their involvement in contests (Radford et al. 2016). Movement patterns can also change in the aftermath of territorial intrusions: for instance, losing groups of white-faced capuchins travelled further, faster and with fewer breaks than did winners following contests with rivals (Crofoot 2013); while, on discovering rival-group feces on their territory, meerkat groups exhibited territory exploration (visiting of sleeping burrows) and dwarf mongoose (*Helogale parvula*) groups decreased their speed of movement and the distance travelled (Jordan et al. 2007; Christensen et al. 2016). Finally, defense of critical resources (roost and nest holes) increased, as did consensus decision-making and group cohesion, in green woodhoopoe groups following extended contests with rival groups earlier in the day (Radford and Fawcett 2014).

Variation in postinteraction behavior in group-living species is likely to be related directly or indirectly to intruder neighbor–stranger identity. For example, where the DE phenomenon occurs, intrusions by strangers may be inherently more stressful than those by neighbors; the former may also elicit stronger defensive responses and longer-lasting contests (Radford 2005). In turn, these factors could result in a greater effect on within-group behavior following intrusions by strangers than neighbors (Radford et al. 2016). Indeed, the immediate defensive response and the level of postinteraction affiliation among green woodhoopoe group members were both demonstrated to be greater following playback of the choruses of strangers versus neighbors (Radford 2005, 2008b). However, defensive responses and postinteraction behavior are not necessarily tightly coupled: while groups of *Neolamprologus pulcher* cichlids were found to respond more aggressively to simulated intrusions of strangers cf. neighbors, there was a greater increase in postinteraction affiliation following the latter (Brintjes et al. 2016). Postinteraction movement patterns may also differ if neighbors and strangers are relatively more or less likely to steal resources. For instance, group-territorial green woodhoopoes spent more time in relevant areas when there are outside threats, perhaps to protect crucial resources (Radford and Fawcett 2014); time in such areas might be expected to be greater following intrusions by strangers who lack such resources (Radford 2005) or following intrusions by neighbors if they are looking to expand their own territories (Müller and Manser 2007). Moreover, the rate of patrolling

different borders, a common territorial behavior (Watts and Mitani 2001), could be influenced by recent intrusion rates by neighbors with whom these borders are shared.

Just like participation in territory defense, levels of postinteraction behavior can differ among individual members of groups (Radford et al. 2016), and some of this variation is likely related to intruder neighbor–stranger identity. For instance, it is predicted that the greater the threat, the more likely it is that there will be rewarding of individuals who assist in defense or punishment of those not helping sufficiently (Radford et al. 2016). Empirical support is provided from green woodhoopoes, where dominant individuals were found to preen subordinates more in the aftermath of simulated intrusions with strangers than neighbors (Radford 2008b); subordinates contribute the most to between-group contests in this species (Radford 2003). Intruder neighbor–stranger identity may also influence the general levels of postinteraction vigilance seen (Olendorf et al. 2004; Descovich et al. 2012): those group members seeking information about mating or dispersal opportunities, or those who are most threatened by the intrusions, might be expected to exhibit greater increases in vigilance. Such variation in postinteraction behavior has likely consequences for individual benefits and costs.

Benefits and costs

Territorial behavior depends on both the benefits and costs of defense; as in any aspect of behavioral ecology, the optimal behavior is a trade-off between the 2. The key benefit to successful defense is retention of resources; losers clearly suffer costs if intruders secure matings, take-over breeding positions, or annex resources such as food, shelters, or the whole territory either temporarily or permanently (Doolan and Macdonald 1996; Kitchen and Beehner 2007; Mares et al. 2011). Even if some or all of a territory is retained, losing groups may avoid particular areas (Stamps and Krishnan 2001), while time spent in zones of conflict may be stressful even if there have been no recent contests (Radford 2011). On an individual level, investment in defense and accrued benefits may also depend on other factors such as duration of stay: for instance, adult territory-holders that are likely to remain there for years will stand to gain more from retaining resources than subordinate individuals that are likely to disperse soon. Since neighbors and strangers often differ in their reasons for intruding (Wilson 1975; Temeles 1994; Müller and Manser 2007), the benefits of defense against each can differ accordingly. Moreover, successful defense may have the additional advantage of reducing the chances that the intruder will return to that territory later, or at least delay the next intrusion (Stamps and Krishnan 1999); that may be particularly beneficial with respect to long-term neighbors compared to strangers who are passing through temporarily.

Responding to territorial intrusions carries other direct and indirect costs which can apply to winners as well as to losers; these costs increase as any interaction escalates in intensity and duration. For instance, physical contests can result in injury or even death (Grinnell et al. 1995; Cant et al. 2002). Moreover, any involvement in defensive activities likely results in increased stress, as well as commitment of time and energy (Hardy and Briffa 2013; Radford and Fawcett 2014; Radford et al. 2016). Not only are these costs borne during interactions themselves, but they can have longer-lasting consequences. For example, the need to recoup lost energetic reserves may lead to reductions in state-dependent cooperative actions, such as sentinel behavior (Bell et al. 2010) and offspring care (Mares et al. 2012), which can negatively affect other group members too. Postinteraction behaviors (see previous section)

can be costly because of inherent trade-offs with other activities. For example, increased vigilance can result in reduced foraging time and food intake (Hollén et al. 2008); greater movement can be energetically costly and can reduce time available for foraging (Janson and Di Bitetti 1997); and border patrols can mean less time spent in core areas which are likely richer in food resources (Arnold et al. 2011). Recent intrusions may also necessitate costly increases in subsequent advertisement of territory ownership (Amrhein and Erne 2006; Benedict et al. 2012).

The extent of these and other costs arising from interactions with intruders or their cues is likely dependent on intruder neighbor–stranger identity. In the simplest sense, the greater the threat presented, the greater the likely costs. The core concept of the DE effect is that the costs associated with a relatively lesser threat of neighbors cf. strangers can be reduced further by a decreased need to respond as strongly when the former intrude (Temeles 1994). However, a full consideration of costs needs to take account of various other factors that have been mostly ignored to date. First, differentiating between intruders may require an initial learning process, where territory-holders must determine threat-level information linked to intruder identity (McGregor 1993). Second, there is the need to maintain the relationship with neighbors once established, and to ensure that they are not cheating by intruding. Such social monitoring may require patrolling behavior or at least time spent near particular borders, leaving core areas or key resources vulnerable to other intruders. If neighbors behave as expected and intrude little, then such costs are kept relatively low and the true benefits of the DE effect become apparent. However, if neighbors increase their intrusion rate, then the assumed benefits of the DE effect may be lessened through the need to retaliate and to respond more strongly in the future (Olendorf et al. 2004; Akçay et al. 2009; Monclús et al. 2014).

MOVING FORWARD

As well as the suggestions made above, here we briefly highlight 3 key areas where significant advances can be made in our understanding of NSRD in group-living species. It is also worth noting that future work should consider territorial responses to “floaters”—individuals that have no fixed territory and are usually found alone (Brown 1969)—as an additional category of outside threat; while floaters occur in many group-territorial species (see, for example, species accounts in Koenig and Dickinson 2004), there has been little investigation of relative responses to them versus neighbors and strangers.

First, there is considerable scope for development of relevant theoretical modeling. Early modeling of animal contests focused on fights between 2 individuals (Kokko 2013); more complex situations tended to be reduced to such a dyadic approach even when more than 2 individuals were involved. More recently, there has been explicit modeling of multiparty contests, including situations where groups face an outside threat either from an individual or a rival group (Sherratt and Mesterton-Gibbons 2013; Rusch and Gavrillets 2017). However, there appears to be practically no theoretical work on the DE and NN effects (Kokko 2013). One exception is Switzer et al. (2001), who use a state-dependent, dynamic modeling approach to consider aggression by territory holders towards intruders. While they do not explicitly model relative responses to neighbors and strangers, they show that residents change their defensive behavior with repeated intrusions, especially if the intruder can be “trained” to stay out of the territory;

the modeling results are equivalent to a change from a NN to DE effect as the relationship with a neighbor develops. Expanding such approaches, especially for group-living species, would help generate testable predictions both about the response levels expected depending on intruder neighbor–stranger identity and which group members might be expected to participate in contests in different circumstances (see Gavrilets 2015 for a review of the use of theoretical models for understanding collective-action problems in heterogeneous groups). Moreover, there needs to be consideration of the effects of intrusions beyond just immediate defensive actions; empirical work is starting to demonstrate that there can be lasting consequences from behavioral interactions in the immediate aftermath through to evolutionary changes (Radford et al. 2016 and references therein), for which there is a concurrent need for mathematical models and evolutionary simulations (Rusch 2014).

Second, while the DE and NN effects have been well studied with respect to behavioral responses, there has been little consideration of potential underpinning physiological mechanisms. Hormones are known to affect and be affected by a variety of social challenges in a range of species, and to be generally important in recognition, territorial aggression, stress, and behavioral interactions (De Dreu 2012; Oliveira and Oliveira 2014). However, we know of only 2 studies that have experimentally compared hormonal responses to neighbors and strangers. In the Mozambique tilapia (*Oreochromis mossambicus*), intrusions by neighbors on the first day of the experiment elicited lower aggression and weaker androgen responses than those by strangers (Aires et al. 2015), in line with DE predictions. Over the course of 4 days, and following repeated territorial intrusions by the same neighbor and different strangers, aggressive responses towards those neighbors approached the level exhibited towards strangers. But, there was a generally lower androgen response on day 4 cf. day 1, and the initial physiological-response difference related to intruder neighbor–stranger identity had disappeared (Aires et al. 2015). By contrast, song sparrow males had higher plasma testosterone levels following playback of neighbors compared to strangers during the incubation period, even though the DE effect was displayed behaviorally (Moser-Purdy et al. 2017b). Clearly much more research is needed on a range of hormones, including various androgens, cortisol and oxytocin (and their analogues), and their interactions (see Aires et al. 2015; Moser-Purdy et al. 2017b and references therein), in different circumstances where fluctuations in responses to neighbors and strangers arise. There also needs to be consideration of both the immediate effects of intrusions and how hormones underpin subsequent consequences in group-living species.

Third, anthropogenic-induced changes in the environment could influence territorial behavior, both in terms of the relative threat presented by different intruders and the ability to discriminate between neighbors and strangers. We provide an example of each case, though the effects of human activities are likely to be wide-reaching (Goudie 2013). As described in “Causes of differences in territorial responses,” one of the within-species factors of importance when considering the relative threat of neighbors and strangers is population density. Habitat loss and fragmentation can have a variety of potential effects in this regard (Bender et al. 1998). For instance, there might be a reduction in population size, which could alter the balance between neighbor and stranger encounters. Alternatively, habitat loss may change territory sizes (e.g., they may become smaller with increasing territory density or larger to provide sufficient food) or increase competition for available resources; consequences could include heightened responses to

neighbors that were previously little threat (Temeles 1994; Sorvari and Hakkarainen 2004; Pratt and McLain 2006; Yoon et al. 2012). Even if there is no change in the numbers of different rivals or the encounter rates with them, human activities could impair accurate assessment of the signals or cues on which differential defensive responses are based (see “Territoriality in group-living species”). For example, anthropogenic noise—the sounds produced by human activities—can have a negative impact on animal communication and the use of environmental cues (Radford et al. 2014; Shannon et al. 2016). While relatively little work has considered territorial behavior directly, there is strong experimental evidence that additional noise can both mask acoustic signals or cues (Nemeth and Brumm 2010) and limit the use of information from other sensory modalities (so-called “cross-modal” effects) because of distraction or stress (Morris-Drake et al. 2016). Complete or partial loss of information about intruder neighbor–stranger identity could disrupt expected DE or NN effects. With anthropogenic changes to the environment occurring at unprecedented rates, the consequences for territorial behavior should not be overlooked.

Testing theoretical predictions, examining underpinning mechanisms, and determining potential impacts of anthropogenic disturbances on territorial behavior requires carefully controlled experimental manipulations. As with any field of behavioral ecology, these should be complemented with natural observations (see Radford et al. 2016 for a discussion of this in the context of out-group conflict in general), but well-designed experiments of course allow stronger conclusions. In some cases, most notably with captive fish and invertebrates, there is the possibility to simulate temporary intrusions by movement of rival individuals or groups into established territories (Batchelor and Briffa 2011; Bruinjes et al. 2016). In species where the relevant cues or signals have been demonstrated to contain identity information, there can be the use of playback (Radford 2005; Herbing et al. 2009) and fecal-presentation experiments (Müller and Manser 2007; Christensen et al. 2016). In both cases, decisions are needed about the number and composition (e.g., sex ratio, dominance structure) of intruders to present, which will depend on the precise question being considered. Since a single playback from a rival only replicates the start of what could be an extended exchange of alternating vocalizations (Radford 2003), interactive playbacks with the experimenter responding in real time to the vocalizations of the focal group are likely to be beneficial (Schmidt et al. 2007). It should be remembered, though, that playbacks cannot fully simulate naturally occurring interactions because the level of involvement exhibited by the study individuals depends on the actions of members of the opposing group (see discussion in Brown and Crofoot 2013). In general, great care must be taken with experimental manipulations in this research field, given the potentially profound and lasting consequences of even simulated between-group conflict (see also Radford et al. 2016).

CONCLUSION

Territorial behaviors in general, and the relative responses to neighbor and stranger intrusions in particular, are not fixed, but represent examples of behavioral flexibility that can be modulated according to the current social environment. Variation and plasticity dependent on intruder neighbor–stranger identity is prevalent in group-living species, where individual group members often do not respond in the same way to one another. Our aim with this review is to stimulate further empirical and theoretical research in this field, thus

building a greater evidence base and knowledge about both territoriality and the evolution and maintenance of social behavior. The neighbor–stranger dichotomy is only one aspect of identity, albeit one with an extensive literature; considering other aspects of identity and factors that moderate responses to intruders (e.g., relative group size, encounter location) will also be beneficial. In discussing a range of fundamental biological issues, including conflict and cooperation, signaling, recognition and discrimination, inter- and intra-specific differences, collective-action problems and decision-making, and cost–benefit trade-offs, we demonstrate that the causes and consequences of variation in group-territorial behavior pertain to a broad suite of research in behavioral ecology. Moreover, since the management and impacts of conflict between groups is of more general importance, including to human society and global politics, we hope the concepts and suggestions for future work in this review will be of broad relevance to a range of other fields.

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